

*MEMORY PROCESSES IN DELAYED SPATIAL
DISCRIMINATIONS: RESPONSE INTENTIONS OR
RESPONSE MEDIATION?*

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Pigeons were trained on a pair-comparison task in which left versus right choices were reinforced following different sequences of two center-key stimuli. Choice accuracy was higher when retention intervals occurred after the entire sequence than when they separated the two stimuli comprising it, and this effect occurred independently of whether the initial and terminal stimuli came from the same or different dimensions. The initial stimulus from the prior trial was a source of proactive interference only in groups for which the retention interval separated the two sequence stimuli. By contrast, differential delay-interval behavior was observed only in groups for which the retention interval followed presentation of the entire sequence. These results indicate that coding processes in delayed discriminations are influenced by the location of the retention interval, and that response mediation affects retention performances if the reinforced choice can be determined prior to the interval.

Key words: response mediation, prospective coding, delayed discriminations, working memory, proactive interference, key peck, pigeons

The present study addressed whether or not pigeons can anticipate their future behavior. Such anticipation, if it occurs, represents a form of prospective coding called *response intentions* (Honig & Dodd, 1986). The idea is that if subjects are exposed to a task in which the stimuli presented early in a trial accurately predict (i.e., regularly precede) different patterns of responding later in a trial, then subjects may learn to remember those stimuli in terms of how they will subsequently respond (Grant, 1982; Roitblat, 1980; Urcuioli & Zentall, 1992). Although this idea sounds plausible, procedures are needed to determine whether or not such prospective coding actually occurs, and how it can be convincingly demonstrated in non-human animals.

Researchers concerned with animal cognition have devised a number of different methods for assessing whether or not subjects can anticipate their own behavior (as well as other forthcoming events). One popular

method has been to compare performances across tasks involving the same stimuli or stimulus sequences but differing in terms of whether or not the events presented prior to the retention interval reliably signal what will occur, or what behavior will be required, after the retention interval. If performances on the retention test differ as a function of the presence versus absence of this predictive relationship, then anticipatory processes are typically inferred to have occurred in the predictive task.

For example, Honig and Wasserman (1981) trained pigeons on delayed successive discriminations in which the stimuli that appeared prior to and following the retention interval (the initial and terminal stimuli, respectively) were equated across groups. For a delayed simple discrimination group, trials beginning with one initial stimulus always ended with reinforcement for pecking whichever terminal stimulus appeared on the retention test, whereas trials beginning with the other initial stimulus never ended in reinforcement. For a delayed conditional discrimination group, whether or not reinforcement was available at the end of a trial depended upon the particular combination of initial and terminal stimuli. In other words, pecking one terminal stimulus but not the other was reinforced on trials beginning with one initial stimulus, and vice versa for trials beginning with the alternative initial stimulus.

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When Honig and Wasserman (1981) later varied the retention interval that separated the initial and terminal stimuli, they found that go versus no-go performances on the retention tests were much more discriminative in the simple discrimination group than in the conditional discrimination group. They interpreted this difference to mean that, given an initial stimulus, birds in the simple discrimination group could anticipate (a) whether or not to peck the forthcoming terminal stimulus (a response intention), (b) whether or not food was scheduled at the end of a trial (an outcome expectancy), or both (see also Honig & Dodd, 1983). Honig and Wasserman's results were later replicated by Urcuioli and Zentall (1990, 1992), who also showed that the higher levels of performance in the simple discrimination group depended upon one initial stimulus predicting food and the other predicting its absence. By contrast, the correlation of those initial stimuli with go versus no-go responding to the terminal stimuli did not matter. Thus, the anticipation of different outcomes (food vs. none) rather than different response patterns appears to account for their results.

Like Honig and Wasserman (1981), Pontecorvo (1985) also inferred anticipatory processes in pigeon working memory on the basis of between-group comparisons. He trained pigeons on a two-alternative forced-choice task in which each trial began with the sequential presentation of two center-key stimuli, an initial (or sample) stimulus and a terminal (or comparison) stimulus. Using red and green hues as stimuli, Pontecorvo reinforced a right-key choice response following matching sequences (i.e., red-red and green-green) and a left-key choice response after nonmatching sequences (i.e., red-green and green-red). The critical manipulation in his experiment involved the location at which the retention interval was placed once birds had acquired this pair-comparison discrimination (Shimp & Moffitt, 1977). For the conditional delayed response (CDR) group, the retention interval followed presentation of the entire sample-comparison sequence, with the two component stimuli separated by 100 ms. For the delayed conditional response (DCR) group, the retention interval occurred between the sample and comparison, with the choice stimuli appearing 100 ms af-

ter the latter. Pontecorvo found that the CDR birds were more accurate in their choices than the DCR birds on trials with long retention intervals. Furthermore, performances in the DCR group were found to be less accurate when the initial (sample) stimulus for a given trial differed from that on the immediately preceding trial, whereas this proactive interference effect was not evident in the CDR group.

Pontecorvo (1985) also interpreted his results as evidence for different working memory codes. Specifically, he inferred that the CDR birds coded which choice response to make (left vs. right) given that the reinforced choice could be discriminated prior to the retention interval and that such response intentions are purportedly easier to remember than what particular stimulus has just occurred (Honig & Thompson, 1982; cf. Konorski, 1959). By contrast, he reasoned that the DCR birds had coded something other than an anticipatory "peck left" versus "peck right" because, for them, the reinforced choice could not be determined until *after* the retention interval. The obvious candidate for the DCR birds would, of course, be the initial stimulus that appeared immediately prior to the retention interval. Indeed, the proactive interference results observed in this group were entirely consistent with the notion that their choices were guided by a retrospective code of red versus green (Wright, Urcuioli, & Sands, 1986; cf. Urcuioli & Zentall, 1986).

Pontecorvo's (1985) findings are certainly provocative, but they are open to other interpretations that do not appeal to anticipatory (prospective) coding. First, because red and green hues were used both as samples and as comparisons, it is possible that the CDR birds simply remembered whether or not the center-key hue stayed the same or changed prior to the retention interval. By this account, all pigeons retrospectively coded the events that occurred prior to the retention interval, but the nature of that code differed between groups because the events themselves differed. In other words, the code for the CDR birds may have been whether the center-key stimulus stayed the same or changed, whereas for the DCR birds, it may have been whether red or green had appeared. This account could also explain why the initial stimulus was

a source of proactive interference in the latter group but not in the former. Moreover, if remembering whether or not something changed is easier than remembering what specific stimulus appeared, this would explain the higher long-delay accuracy in the CDR group.

A second alternative, compatible with the first, is that the CDR birds performed more accurately at long retention intervals because they developed explicit mediational behavior during the retention interval (cf. Blough, 1959; Zentall, Hogan, Howard, & Moore, 1978). Pontecorvo (1985) explicitly discounted this explanation of his results, noting that although the CDR birds did periodically peck the left or right key during the retention interval, such behavior did not occur consistently enough to account for their performances. However, given that only key pecking was recorded, it is possible that other overt forms of mediation (e.g., standing in front of the left or right key) occurred with greater regularity during the retention interval and, thus, significantly contributed to performances in this group.

In order to evaluate the first alternative interpretation, the present study replicated the two conditions of Pontecorvo's (1985) experiment but included two additional groups in which different stimuli were used as samples and as comparisons in the two-stimulus center-key sequence. For the latter groups, the initial and terminal stimuli always differed, so stimulus change could not be a cue for choice. However, coding which choice response to make after the retention interval was possible for one of these groups because for them, as in Pontecorvo's CDR condition, both stimuli appeared prior to the retention interval. Of interest was whether or not they too would show better accuracy on the retention test relative to a corresponding DCR group in which a retention interval separated the two center-key stimuli. If so, this would provide better support for the response-intention explanation by showing that enhanced accuracy in a CDR group does not require retrospective coding of the presence versus absence of stimulus change. Of course, the possibility of response mediation still remains.

Regarding this second alternative, we also observed the retention-interval behavior of

every pigeon during two mixed-delay sessions that followed the retention tests. This allowed us to assess whether or not more accurate working memory performances in CDR groups could arise because differential delay-interval behavior other than key pecking provides an additional cue for the choices made on the retention test (cf. Blough, 1959; Zentall et al., 1978).

METHOD

Subjects

Sixteen experimentally naive White Carneau pigeons obtained from the Palmetto Pigeon Plant served in the experiment. All were retired breeders (i.e., older than 6 years) and were housed in individual stainless-steel cages in a colony room with a 14:10 hr light/dark cycle. Upon arrival in the laboratory, birds were given unlimited access to food in order to establish their free-feeding body weights. Immediately prior to the start of the experiment, each pigeon was gradually reduced to 80% of its free-feeding weight by restricted feeding. In addition, they were randomly assigned to one of four groups described below. Grit and water were always available in the home cages.

Apparatus

Two identically configured BRS/LVE pigeon chambers were used in the experiment. Each chamber consisted of a sound-attenuating enclosure (Model SEC-002) equipped with a Model PIP-016 intelligence panel. Three horizontally aligned, clear plastic pecking keys were mounted behind 2.5-cm circular holes that were located 25.5 cm above the chamber floor and were spaced approximately 8.3 cm apart, center to center. Mounted behind each key was a 12-stimulus inline projector (Model IC-901-IDD). The center-key projector was equipped with BRS/LVE Film Pattern No. 692 to display red, green, and white homogeneous fields, three white vertical lines on a black background, and a filled white dot. The side-key projectors displayed only the white homogeneous field (Pattern No. 692). A rear-mounted grain magazine was accessible through an opening (5.0 cm by 5.8 cm) centered 13 cm below the center key. General illumination for the pigeon's compartment in the chamber (37 cm high by 30

<u>P-CDR</u>	<u>P-DCR</u>
R-R → Left +	R—R → Left +
R-G → Right +	R—G → Right +
G-R → Right +	G—R → Right +
G-G → Left +	G—G → Left +

<u>U-CDR</u>	<u>U-DCR</u>
R-V → Left +	R—V → Left +
R-D → Right +	R—D → Right +
G-V → Right +	G—V → Right +
G-D → Left +	G—D → Left +

Fig. 1. Retention test contingencies for the four experimental groups. CDR = conditional delayed response task, DCR = delayed conditional response task. P and U prefixes indicate replication of contingencies used by Pontecorvo (1985) and the current (Urcuioli) modification of them, respectively. R = red, G = green, V = vertical lines, and D = dot stimuli. The four possible center-key sequences are shown to the left of the arrows, and the reinforced side-key choice is shown to the right of the arrows (counterbalancing not shown). Location of the retention interval is identified by the longer lines in each row.

cm wide by 34 cm long) was provided by a partially covered houselight (GE No. 1829 bulb) located 7.6 cm above the center key. The opening in the houselight cover was positioned such that light was directed toward the ceiling. Ventilation and interior masking noise were provided by a continuously running blower fan mounted on the outside of the chamber. Experimental events in both chambers were controlled and recorded by a single Zenith PC-AT microcomputer.

Procedure

Preliminary training. Following initial magazine training, all birds were shaped by the method of successive approximations to peck a white center-key stimulus. After roughly 60 to 90 reinforced pecks to this stimulus, preliminary training began, during which birds learned to peck red and green on the center key and, in separate sessions, the vertical lines and the dot. The first five of these sessions involved 30 presentations each of the two hues in random order. Food reinforcement was contingent upon two pecks to each center-key hue during the first session, three pecks during the second session, five during the third, and 10 during the fourth and fifth

sessions. The last two preliminary training sessions involved the vertical and dot stimuli with food reinforcement contingent upon two and five pecks, respectively, in each session. Successive stimulus presentations in all sessions were separated by a 10-s intertrial interval (ITI), the first 9 s of which was spent in darkness. The houselight came on for the last 1 s of the ITI and remained on for the duration of the trial (including food reinforcement). Food reinforcement duration was constant within a session but varied across sessions and across birds in such a way as to maintain 80% body weights as closely as possible. These durations ranged from 2 to 6 s.

Acquisition. Next, all birds were trained on a delayed pair-comparison task similar to that used by Pontecorvo (1985; see also Shimp & Moffitt, 1977). In this task, trials consisted of successive presentations of two stimuli on the center key followed by a choice between the left and right side keys. For the birds assigned to the Pontecorvo (P) groups (see Figure 1), both the first and second center-key stimulus that appeared prior to choice were either red or green hues. For the birds assigned to the Urcuioli (U) groups, the first stimulus in the sequence was either red or green and the sec-

ond stimulus was either vertical or dot. The four possible two-stimulus sequences for each group were randomized and were presented equally often in each 96-trial training session.

Training trials began with an initial or sample stimulus (red or green) appearing on the center key. The first peck to this stimulus initiated a 5-s observation period. The first sample peck after 5 s then turned the center key off for 100 ms and produced the terminal or comparison stimulus in the sequence. For all groups, five pecks to the comparison stimulus turned it off and, following a 100-ms interval, produced a white light on each of the two side keys. A single peck to either side key then turned both lights off and produced either food reinforcement (if the choice was correct) or an equivalent timeout period with the houselight turned off (if the choice was incorrect). For half of the P birds, a left side-key choice was correct (reinforced) following the two matching center-key sequences (i.e., red-red and green-green), whereas a right side-key choice was correct following the two mismatching sequences (red-green and green-red). The remaining P birds had the opposite contingencies. For the U birds, the choice contingencies were likewise counter-balanced across the four sequences consisting of the red versus green sample stimulus and the vertical versus dot comparison stimulus.

An incorrect choice on any trial caused that trial to be repeated with the same reinforcement contingencies in effect as on non-correction trials. However, no data from the correction trials were included in any computations or analyses. The duration of food reinforcement for correct choices continued to be adjusted on a daily basis for each bird so as to maintain its 80% body weight. Successive trials were again separated by a 10-s ITI, the first 9 s of which was spent in darkness.

Each bird was trained on its respective task until it made 90% or more correct choices in five of six consecutive training sessions. At that point, retention testing was begun. Three subjects (1 in the P groups and 2 in the U groups) failed to reach the acquisition criterion after 40, 50, and 55 sessions, respectively, but were nevertheless tested because they exhibited high and stable accuracy levels (91.0%, 89.6%, and 87.3% correct, respectively, over the last five training sessions).

Retention testing. Retention tests were conducted in two 20-session blocks. In the first (short-delay) block, the retention intervals were 0, 2, 4, and 8 s; in the second (long-delay) block, they were 0, 4, 8, and 16 s. The four retention intervals in each block were randomized across trials with the restriction that each occur equally often with each of the four center-key sequences. For birds assigned to the CDR conditions (P-CDR and U-CDR), delays occurred between the comparison stimulus and the side-key choices (see Figure 1). For birds in the DCR conditions (P-DCR and U-DCR), delays occurred between the sample and comparison stimuli. All other procedural details were identical to those during acquisition except that pecking an unlit side key during any retention interval immediately turned off the houselight and restarted the trial. This latter contingency was designed to discourage explicit anticipatory choice responding.

Observational sessions. The sessions during which the bird's delay-interval behavior was observed were generally conducted 3 to 7 weeks after completion of the long-delay retention tests. In preparation for the observational sessions, birds were retrained with the long-delay set for a minimum of three sessions and until they recovered the accuracy levels formerly exhibited with this set. At that point, each bird was studied for two additional long-delay sessions, during which their behavior during the retention interval was observed and recorded on 20 successive trials (Trials 40 through 59). One of us made the observations on one day, and the other made the observations on the following day.

To standardize the observational procedure and criteria, each observer recorded instances of (a) any pecking during the delay interval (including where such pecking was directed), (b) any movement away from the center key toward one or the other side key (or toward the left or right side of the chamber), and (c) any other distinctive movement (e.g., change in head position). Each observer positioned himself by the chamber window such that he could not see the center-key stimulus or stimuli that occurred prior to the retention interval, although pecking at the center key was easily seen. The entire retention interval was then observed prior to writing down the observations for that interval.

Retention intervals of 0 s were simply recorded as such, and no behavioral observations were made. Also noted was whether the subsequent choice response was correct or incorrect. The observations made by each of us were communicated to the other only after both had had the opportunity to separately record the delay-interval behavior for a given bird. In addition, each observer separately tallied the major kinds of delay-interval behavior that were exhibited by each bird as a function of the preceding sample (for the DCR birds) or sample sequence (for the CDR birds) for later comparison.

Across the two observational sessions, there were 10 4-s retention intervals, 11 8-s retention intervals, and 11 16-s retention intervals, thus yielding a total of 32 delay-interval observation periods. (Again, no observations were made on the remaining eight 0-s delay trials.) Of those trials on which observations were made, 15 required one spatial choice (e.g., left) for reinforcement and 17 required the other (e.g., right).

RESULTS

For all statistical analyses reported below, Type I error rate was set at .05 using the tabled *F* values reported by Rodger (1975). Rodger's tabled values set error rate on a per-decision (as opposed to an experiment-wise) basis for post-hoc contrasts selected following an overall analysis of variance (ANOVA).

Acquisition

Although not all birds reached the 90% acquisition criterion, the four groups were nonetheless very similar in choice accuracy immediately prior to retention testing. Averaged over the last five training sessions for each bird, accuracy ranged from 92.1 to 93.7% across groups. ANOVA showed no significant between-group differences in the terminal accuracy levels, $F(3, 12) = .29$. Thus, steady-state performance on the delayed pair-comparison task with no appreciable retention interval did not vary as a function of whether the sample and comparison stimuli were from the same (P groups) or different (U groups) dimensions.

Retention Performances

The primary dependent measure chosen for presentation and analysis of the retention

results is A' , a nonparametric index of recognition accuracy (Grier, 1971; Pollack & Norman, 1964). This performance index was selected because it was the measure reported by Pontecorvo (1985), thus facilitating any desired comparisons with his data. A' values were computed for individual subjects by defining *hits* as correct choices following the two matching sequences of center-key stimuli in the P groups or following the corresponding sequences in the U groups (see Figure 1). *False alarms* were defined as the same spatial choices following the nonmatching sequences in the P groups or their equivalents in the U groups. For each bird, hits and false alarms were cumulated by delay over all 20 sessions of the short- and the long-delay tests prior to computing A' . The formula for A' when hits (H) exceed false alarms (FA) is

$$A' = 0.5 + \frac{(H - FA)(1 + H - FA)}{4H(1 - FA)}.$$

When hits equal false alarms, $A' = 0.5$; when hits are less than false alarms, then

$$A' = 0.5 - \frac{(FA - H)(1 + FA - H)}{4FA(1 - H)}.$$

The short-delay retention data (not shown) indicated that although choice accuracy declined with increasing delays, there was little variation in performance across groups. ANOVAs comparing performances in the two CDR groups and in the two DCR groups revealed no significant within-task differences, $F_s(1, 6) = 0.11$ and 0.23 , respectively. Moreover, an ANOVA comparing the combined CDR data with the combined DCR data likewise showed no significant overall difference between conditions, $F(1, 14) = 0.00$.

In contrast to these results, the long-delay data revealed clear and substantial between-group differences in retention. As shown in Figure 2, working memory performances were more accurate in the CDR than in the DCR groups at every delay beyond 0 s. Initial ANOVAs comparing performances of the two CDR groups with one another and performances of the two DCR groups with one another showed no significant within-task differences, $F_s(1, 6) = 0.06$ and 0.46 , respectively. In view of this, the data from each task were combined for further analyses

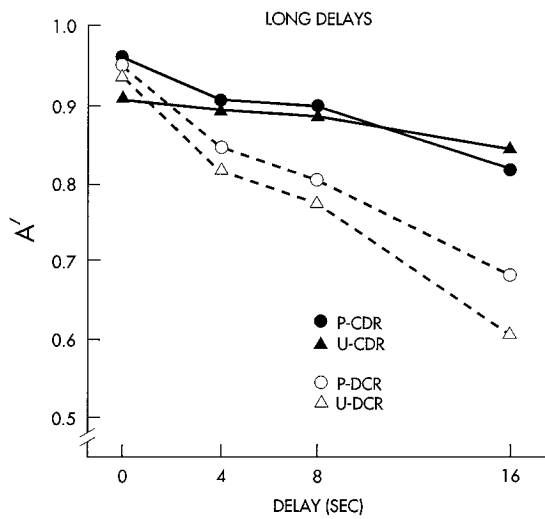


Fig. 2. Mean values of A' for the four experimental groups averaged over all 20 sessions of retention testing with the long-delay set.

which confirmed that choice accuracy was higher overall in the CDR than in the DCR condition, $F(1, 14) = 6.39$. The overall effect of delay was significant, $F(3, 42) = 62.58$, as was the Condition \times Delay interaction, $F(3, 42) = 17.50$, which reflected the increasing disparity in performance between the CDR and DCR conditions with increasing delays. Table 1 shows the individual A' data for all 16 birds.

Proactive Interference Effects

Trial-by-trial analyses were conducted on the short- and long-delay data in order to identify possible sources of intertrial proactive interference (Wright et al., 1986). In view of Pontecorvo's (1985) finding that CDR and DCR performances differ primarily in their sensitivity to the effect of prior samples, we computed choice accuracy on trial n as a function of whether the trial $n - 1$ sample was the same or different. This computation was further broken down by the trial n delay, and the results were cumulated over all 20 sessions with each set of delays. For all birds, the sample was considered to be the initial red or green stimulus of the center-key sequence.

The results of these analyses are shown in Figure 3. In each panel, the filled symbols show trial n accuracy when the sample for that trial was the same as that on trial $n - 1$ ($S = S$). The open symbols plot the corresponding

Table 1

A' values by delay averaged over the 20 retention test sessions with long delays.

Group	Bird	Delay (s)			
		0	4	8	16
CDR	P1	.93	.88	.85	.78
	P2	.93	.83	.80	.62
	P3	.98	.98	.98	.96
	P4	.98	.96	.97	.96
	<i>M</i>	.96	.91	.90	.83
	U1	.96	.92	.90	.83
	U2	.89	.84	.82	.80
	U3	.92	.95	.92	.90
	U4	.86	.90	.91	.88
	<i>M</i>	.91	.90	.89	.85
Overall (CDR) <i>M</i>		.93	.91	.89	.84
DCR	P5	.96	.80	.77	.65
	P6	.90	.73	.70	.57
	P7	.98	.95	.93	.81
	P8	.97	.91	.85	.72
	<i>M</i>	.95	.85	.81	.69
	U5	.94	.79	.82	.63
	U6	.97	.89	.82	.64
	U7	.96	.89	.83	.69
	U8	.88	.70	.67	.48
	<i>M</i>	.94	.82	.78	.61
Overall (DCR) <i>M</i>		.94	.83	.80	.65

accuracy when the samples for two successive trials differed ($S \neq S$). The data for the CDR and DCR conditions in Figure 3 were averaged across the P and U groups because overall retention was very similar across the two groups in each condition (see Figure 2) and, more important, because initial analyses indicated that the pattern of trial-by-trial effects did not differ within conditions. The combined results show a very clear difference between the CDR and DCR conditions in the effect of prior samples. In the CDR condition, accuracy during both the short- and long-delay tests was unaffected by the correspondence, or lack thereof, between the trial n and trial $n - 1$ samples. By contrast, choices by the DCR birds were clearly less accurate when the trial n sample differed from the trial $n - 1$ sample. In other words, for the DCR condition, intertrial proactive interference was created when the alternative hue sample had been presented on the immediately preceding trial.

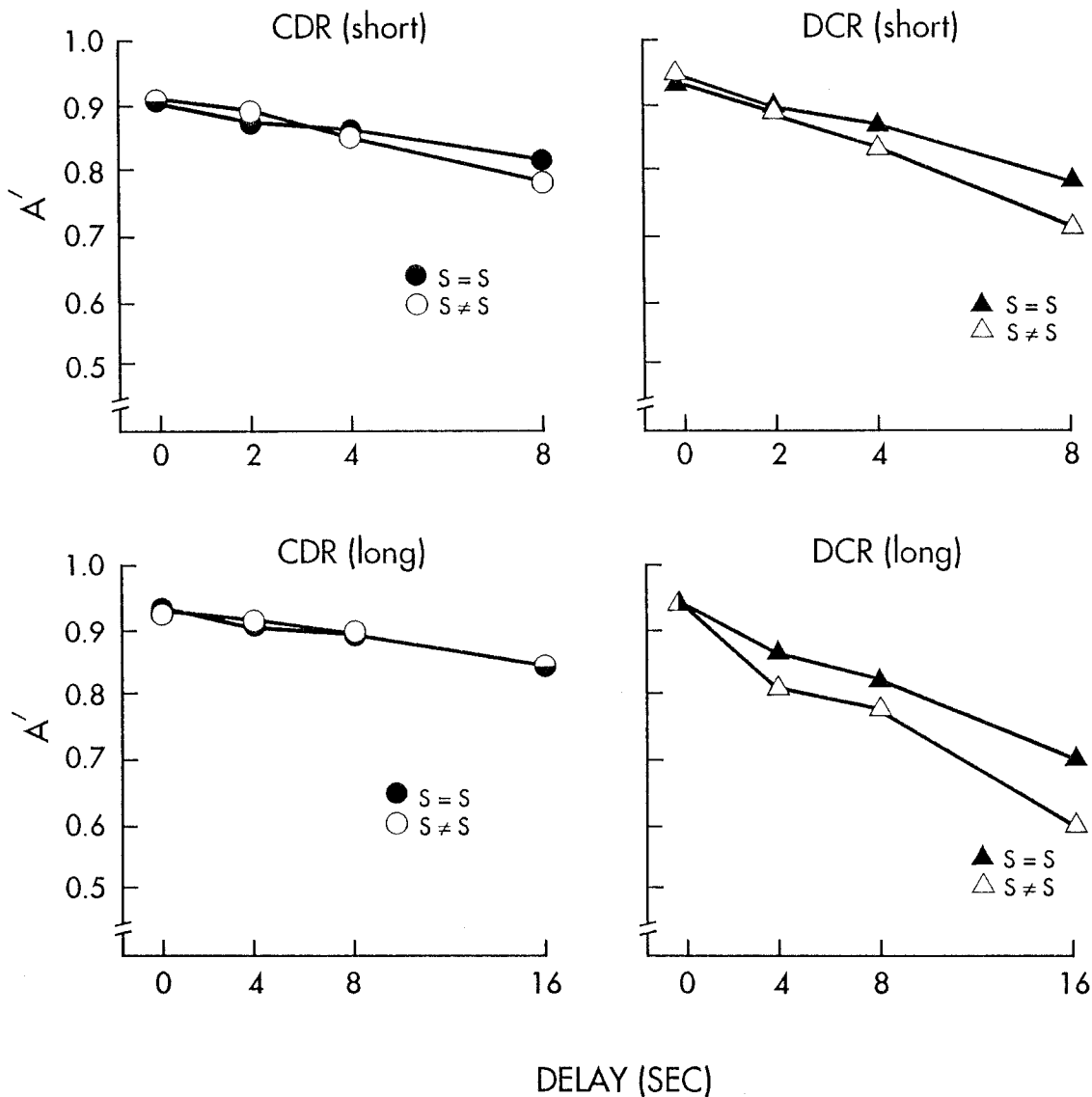


Fig. 3. Mean A' values for the combined CDR groups (left panel) and the combined DCR groups (right panel) on trials in which the sample was the same as that on the immediately preceding trial ($S = S$) versus trials in which the sample differed from that on the immediately preceding trial ($S \neq S$). Data are shown separately for the 20 sessions of short-delay retention testing (top panels) and for the 20 sessions of long-delay retention testing (bottom panels).

ANOVAs showed that the effect of same versus different samples on choice accuracy was not significant in the CDR condition for either short or long delays, $F_s(1, 7) = 1.85$ and 0.16 , respectively, nor did this variable interact with delay, $F_s(3, 21) = 1.73$ and 0.95 , respectively. By contrast, ANOVAs on the DCR data confirmed that overall accuracy on different-sample trials was significantly lower

than on same-sample trials, $F_s(1, 7) = 10.27$ and 41.62 for the short- and long-delay sessions, respectively. Furthermore, the same versus different variable did interact with delay in this condition, $F_s(3, 21) = 2.64$ and 4.32 , respectively, indicating that a prior competing sample produced relatively greater interference at the longer delays within each set.

Table 2

A' values by delay for the CDR birds on trials in which the initial stimulus was the same as or different from that on the preceding trial.

CDR bird	Trial type	Short delay (s)				Long delay (s)			
		0	2	4	8	0	4	8	16
P1	Same	.80	.87	.87	.76	.94	.87	.84	.81
	Different	.92	.88	.83	.72	.93	.88	.86	.75
P2	Same	.89	.74	.72	.72	.93	.82	.79	.63
	Different	.82	.81	.68	.55	.93	.84	.82	.60
P3	Same	.95	.97	.97	.93	.96	.98	.98	.96
	Different	.95	.96	.97	.94	.98	.98	.98	.96
P4	Same	.92	.92	.90	.85	.98	.96	.97	.95
	Different	.94	.92	.89	.84	.99	.96	.97	.96
U1	Same	.94	.86	.85	.76	.94	.91	.90	.83
	Different	.90	.90	.86	.67	.97	.92	.91	.83
U2	Same	.87	.82	.88	.83	.93	.83	.83	.77
	Different	.87	.83	.84	.81	.87	.85	.83	.82
U3	Same	.96	.90	.89	.84	.90	.95	.92	.90
	Different	.93	.91	.87	.84	.92	.96	.92	.89
U4	Same	.96	.92	.89	.87	.90	.89	.91	.88
	Different	.96	.90	.92	.88	.82	.90	.92	.89

Tables 2 and 3 show individual same-versus-different-trial performances in each condition during the short- and long-delay retention tests. For each condition and delay set, there are 32 possible comparisons of accuracy

when the trial n sample was the same as versus different from the trial $n - 1$ sample. In the CDR condition (Table 2), different-trial accuracy was lower than same-trial accuracy in only 14 of the 32 comparisons with the short

Table 3

A' values by delay for the DCR birds on trials in which the initial stimulus was the same as or different from that on the preceding trial.

DCR bird	Trial type	Short delay (s)				Long delay (s)			
		0	2	4	8	0	4	8	16
P5	Same	.94	.83	.72	.66	.97	.83	.74	.73
	Different	.91	.83	.77	.56	.95	.77	.80	.54
P6	Same	.93	.84	.81	.72	.90	.77	.70	.60
	Different	.93	.81	.78	.63	.89	.69	.73	.53
P7	Same	.97	.97	.93	.87	.99	.96	.95	.87
	Different	.98	.92	.90	.73	.98	.94	.90	.75
P8	Same	.98	.90	.93	.87	.99	.92	.89	.75
	Different	.96	.93	.92	.83	.97	.90	.82	.68
U5	Same	.94	.91	.91	.77	.95	.82	.86	.65
	Different	.95	.92	.87	.84	.93	.77	.78	.65
U6	Same	.97	.94	.91	.79	.97	.92	.89	.68
	Different	.96	.93	.88	.81	.97	.87	.74	.61
U7	Same	.97	.94	.92	.88	.96	.89	.86	.75
	Different	.95	.95	.90	.71	.95	.89	.80	.60
U8	Same	.89	.85	.81	.67	.88	.79	.72	.55
	Different	.87	.83	.70	.59	.86	.65	.61	.40

Table 4

A' values averaged over delay for each group over the last two long-delay and recovery sessions and the two observational sessions.

Group	Sessions		
	Long delay	Recovery	Observational
P-CDR	.92	.90	.90
U-CDR	.87	.92	.90
P-DCR	.86	.88	.86
U-DCR	.83	.86	.86

delays, and in only 6 of 32 comparisons with the long delays. By contrast, in the DCR condition (Table 3), there were 22 instances of lower accuracy on different trials than on same trials with the short delays and 27 instances with the long delays. Clearly, proactive interference from a competing prior-trial sample was consistently observed only in the DCR subjects.

Delay-Interval Behavior

The observations of delay-interval behavior were made at various times following completion of the retention tests. In preparation for these sessions, each bird was retrained with long delays until its performance recovered to a level similar to that seen at the end of the retention testing. Table 4 shows the A' values for the last two recovery sessions averaged over delays and over the 4 birds in each group. Also shown are the corresponding A' values for the last two sessions of long-delay testing and for the two observation sessions. These values show that performances were stable within groups and that the two CDR groups continued to maintain higher overall accuracy levels than the two DCR groups.

The observational data indicated that none of the birds in the P-DCR and U-DCR groups behaved differentially during the retention intervals following the red versus green samples. For example, all 4 P-DCR birds pecked at or stood in front of the dark center key during the retention interval following each sample. Similarly, 3 of the 4 U-DCR birds pecked at the dark center key during the retention intervals; the remaining bird pecked at or "bit" the houselight. Table 5 presents a statistical summary of the frequency of these kinds of behavior for the 8 DCR birds. The table shows the total number of trials over the

Table 5

Number of trials (of total) in which the indicated delay-interval behavior was observed following each sample for the DCR birds.

DCR bird	Delay-interval behavior	Sample	
		Red	Green
P5	Stands in front of and/or pecks at center key	16/16	16/16
P6	Pecks at or around the center key	16/16	13/18
P7	Pecks at or above center key	15/15	17/17
P8	Pecks dark center key and raises head above it	15/15	16/17
U5	Raises head toward houselight with occasional center-key pecks	16/17	13/15
U6	Pecks the center key	15/15	17/17
U7	Pecks center key, then paces back and forth along intelligence panel	14/15	13/17
U8	Pecks at and "bites" houselight	13/15	16/17

two observational sessions in which the indicated delay-interval behavior occurred. For example, during the retention intervals that followed a red sample, Bird P6 pecked at or around the dark center key on 16 of such trials (out of a possible 16 trials) and exhibited the same behavior on 13 of 18 green-sample trials. Given that the frequency of the dominant delay-interval behavior was essentially the same following both samples, the choices of the DCR birds following the retention interval (see Figure 2) are not attributable in any obvious way to these responses.

By contrast, 7 of the 8 CDR birds exhibited delay-interval behavior that was clearly differential with respect to the preceding sample-comparison sequence. In other words, the dominant behavior observed during the retention intervals following the two sequences that were discriminative for a left choice response was noticeably different from that observed following the two right choice sequences. Tables 6 and 7 present these data for the individuals in the P-CDR and U-CDR groups, respectively; the sample-comparison sequences preceding the retention interval are labeled according to the reinforced choice response (left vs. right) associated with them. The tables show the number of times following each sequence that birds exhibited the delay-interval behavior described on the left. For example, Bird P3 pecked in front of

Table 6

Number of trials (of total) in which the indicated delay-interval behavior was observed following sample-comparison sequences discriminative for left versus right choices for the P-CDR birds.

Bird	Delay-interval behavior	Sequence	
		Left	Right
P1	Moves toward left key with occasional center-key pecking	12/17	2/15
	vs. Moves toward right key	3/17	13/15
P2	Pecks wall between center and left key	8/14	5/17
	vs. Pecks center key and houselight	6/14	12/17
P3	Pecks in front of left key	16/17	0/15
	vs. Pecks dark center key	1/17	14/15
P4	Pecks around left key	13/15	0/13
	vs. Pecks center key	2/15	13/13

the left key during the retention interval on 16 of the 17 trials that began with the sample-comparison sequences associated with a left reinforced choice. On the other hand, this behavior was never observed during the retention interval on the 15 trials that began with the sequence associated with a right reinforced choice. By contrast, Bird P3 pecked

the dark center key during the retention interval on 14 of 15 right sequence trials, whereas center-key pecking during the retention interval was observed on only 1 of the 17 left sequence trials. The differential nature of the delay-interval behavior observed in the CDR groups can be quickly appreciated by comparing the frequencies along the main diagonal in each bird's table with the frequencies along the minor diagonal. For every bird, the former is larger than the latter. The 1 bird that showed the least differential pattern of delay-interval behavior (Bird P2) was also the bird with the lowest overall choice accuracy in the CDR condition.

Also noteworthy was the finding that when the delay-interval behavior exhibited by a CDR bird was appropriate to the *opposite* sample-comparison sequence, it very often made an incorrect choice on the subsequent retention test (not shown in the tables). Across all CDR birds except Bird P2, an incorrect choice occurred 18 times out of the 25 occasions in which the opposite delay-interval behavior was apparent. Stated otherwise, on 18 of these 25 occasions, birds chose the side key that was appropriate to their preceding delay-interval behavior (albeit inappropriate to the sample-comparison sequence). In passing, we should also point out that the CDR birds very rarely, if ever, showed the compo-

Table 7

Number of trials (of total) in which the indicated delay-interval behavior was observed following sample-comparison sequences discriminative for left versus right choices for the U-CDR birds.

Bird	Delay-interval behavior	Sequence	
		Left	Right
U1	Moves back and forth between center and left keys	9/15	0/17
	vs. Moves back and forth between center and right keys or along entire front panel	5/15	16/17
U2	Pecks below and to left of center key	10/15	2/17
	vs. Pecks below center key toward food magazine	5/15	15/17
U3	Moves toward left key	11/17	3/15
	vs. Moves toward right key	6/17	12/15
U4	Pecks houselight and/or moves to left	16/16	0/16
	vs. Pecks center key and/or moves to right	0/16	16/16

nents of both delay-interval patterns in a single trial.

DISCUSSION

This experiment reproduced the two major features of Pontecorvo's (1985) study. First, birds for which both center-key stimuli appeared prior to the retention interval showed more accurate working memory performances with long delays than did the birds for which the retention interval intervened between the first and second stimulus. Second, choice accuracy in the latter (DCR), but not in the former (CDR), condition was sensitive to the sample that appeared on the immediately preceding trial. Specifically, the DCR birds were less accurate in their retention-test choices on trials that involved a sample opposite to the one on the prior trial.

The present study also showed that these effects occurred whether the same or different stimuli were used as samples and as comparisons. In Pontecorvo's (1985) study, both sets of stimuli were red and green hues, so the birds in his CDR condition may have coded whether the center-key stimulus stayed the same or changed prior to the retention interval. As mentioned earlier, this could potentially explain why these birds were more accurate in their long-delay choices than the DCR birds were. Moreover, such a retrospective code would be insensitive to the particular sample stimulus from the immediately preceding trial, a point confirmed by the lack of intertrial proactive interference from this source in Pontecorvo's CDR data.

One contribution of the present study, then, was to show that the CDR versus DCR differences reported by Pontecorvo (1985) can arise by means other than different retrospective codes. Specifically, if the proactive interference observed in both of our DCR groups reflects retrospective coding of the hue samples (Wright et al., 1986), then the corresponding data from our CDR groups along with their higher overall levels of retention suggest that the CDR birds may very well have been *prospectively* coding their left versus right choices. We would also have to assume, of course, that such response intentions are more memorable than red versus green sample stimuli in order to explain the higher levels of choice accuracy in the CDR groups, but

that assumption would be in line with previous statements that prospective codes are generally more durable than retrospective codes (e.g., Honig & Dodd, 1986; Honig & Thompson, 1982; Wasserman, 1986).

The second contribution of the present study was to show that CDR birds behaved differently during the retention interval as a function of whether a left or right choice would subsequently be reinforced. By contrast, the delay-interval behavior of the DCR birds was nondifferential. The correlation between the presence versus absence of differential delay-interval behavior and the between-group differences in long-delay accuracy thus suggests another possible explanation for more accurate retention performances in the CDR groups: Their choices may have been directly cued by their differential delay-interval behavior. Such behavior, by persisting throughout the retention interval, should support higher levels of accuracy because at the time of choice, the cue arising from it would likely be much stronger than that provided by the hypothesized retrospective (red vs. green) codes for the DCR groups.

The potentially mediating properties of delay-interval behavior in animal working memory have long been recognized (e.g., Blough, 1959; Fletcher, 1965; Hunter, 1913; Zentall et al., 1978). Zentall et al., for instance, found a positive correlation between the presence versus absence of differential delay-interval behavior and accuracy in pigeons' delayed matching. Indeed, he reported that this experimentally uncontrolled variation in delay-interval behavior across subjects was a better predictor of delayed matching than the experimentally manipulated sample-response contingencies of interest in his study.

The observational results obtained here, in conjunction with those of Zentall et al. (1978), bring into question the necessity of appealing to response intentions in order to account for our CDR-DCR differences and those previously reported by Pontecorvo (1985). In other words, response mediation may be sufficient to account for the CDR performances. Certainly, the potential cue properties of the differential delay-interval behavior were quite apparent on trials in which the observed behavior was the opposite of that typically observed following left and right

sample sequences. Over 60% of those trials ended in an incorrect choice, thus indicating that the discriminative aspects of the delay-interval behavior were powerful enough to override any cue associated with the sample-comparison sequence itself.

One objection to this response-mediation alternative is that it fails to explain how the differential behavior developed in the first place. In other words, might the bird's anticipation of its subsequent choice (i.e., a response intention) itself be the origin of such behavior? The problem with this, of course, is that the origins of the response intention may very likely be the same as those underlying the differential delay-interval behavior. If so, then the response-intention notion is superfluous. In this light, it is of interest to note that the 1 CDR bird for which the delay-interval behavior was least differential was also the bird with the least accurate choice performance.

In sum, hypothesizing response intentions seems to add nothing to the fact that when one choice is regularly reinforced following certain sequences and the opposite choice is regularly reinforced following other sequences, components of those choice patterns become conditioned to the sequences themselves such that they appear prior to actual choice. Those anticipatory (i.e., conditioned) patterns of responding may, in turn, provide another cue for choice besides the visual aspects of the initiating sequence.

This analysis is not meant to suggest that all working memory tasks that involve predictable outcomes or forthcoming behavior can be explained in this manner, or that prospective coding as normally conceived has no demonstrable impact on animal working memory. However, the necessity of postulating such a coding process in the present situation seems to require evidence for response intentions that is *independent of* overt, differential delay-interval behavior. If it could be shown, for example, that choice predictability prior to the retention interval enhances the accuracy of working memory performance even in the absence of differential delay-interval behavior, a stronger case for response intentions could be made. Unfortunately, ruling out the occurrence of such differential behavior may be impossible in delayed spatial discriminations given the possibility of very fine differences in spatial or-

ientiation during the retention interval. A more suitable approach would be to use non-spatial working memory tasks like delayed matching to sample or delayed successive discriminations of the type used by Honig and Wasserman (1981). However, current evidence from between-group comparisons of working memory (Urcuioli & Zentall, 1990) and from within-group transfer-of-control tests (Urcuioli & Zentall, 1992) suggests that in delayed successive discriminations, response intentions are not a factor. Perhaps we can safely relinquish this idea for delayed spatial discriminations too.

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